Synthesis 2: Tool use in Chimpanzees

Background

Tool use has been incalculably influential in the evolutionary and ecological success of humans. Tools allow us to manipulate our environment to evade pathogens, defend against predators, produce food, and build shelters. While many consider this trait to be a defining characteristic of humans, tool use has actually been documented in diverse clades throughout the animal lineage, from insects to fish to birds (Biro et al., 2013). However, chimpanzees (*Pan troglodytes*) use tools with greater variability in form and function than any other species besides humans. Thus, tool use in *Pan troglodytes* serves as a valuable model for tool use in all species. The existing research to date suggests that tool usage primarily allows chimpanzees to increase their exploitation of food resources such as ants, termites, and nuts. Additionally, while factors such as ecological opportunity, dexterity, and intelligence are all necessary for the emergence of tool use, sociality is necessary for the transmission of that knowledge across generations.

Pan troglodytes has been observed to use a variety of tools in a wide range of contexts from social displays to self-cleaning, but use of feeding tools is the behavior that has been most consistently and commonly documented in the wild (Boesch and Boesch, 1990). *Pan troglodytes* lives primarily in rainforests, which experience significant seasonal shifts in resource availability that could influence the use of feeding tools. *Pan troglodytes* most commonly will obtain and modify stick or stone tools to assist with preying on ants, obtaining grubs and honey, and emptying nuts. Insight into the evolutionary pressures that resulted in the origin of tool use in chimpanzees will shed valuable insight on the source of within- and between-species variation in tool use, how tool use began, and why it arose in so few primate species overall.

Effect of Ecology on Tool Use Evolution

Currently, two hypotheses dominate the literature regarding the ecological conditions that facilitated the evolution of tool usage. The first is the idea that tool use originated out of necessity for foraging strategies for alternative food sources when preferred resources were unavailable (Sanz and Morgan, 2013). This hypothesis will hereafter be referred to as the "necessity hypothesis." It has been proposed that preferred foods exert a different selection pressure on organisms than "fallback foods" that are consumed under conditions of scarcity (Marshall and Wrangham, 2007). For example, preferred foods might affect feeding adaptations and cognitive traits related to foraging, whereas fallback foods tend to require more specialized traits (Sanz and Morgan, 2013). This is because fallback foods may have evolved more significant defenses against primate consumption than preferred foods. Thus, the necessity hypothesis posits that tool use evolved as a response to resource scarcity, allowing *Pan troglodytes* to exploit fallback foods when preferred foods are less available.

Long-term field observations of wild chimpanzees yield conflicting results regarding the necessity hypothesis. In support of the role of necessity, a chimpanzee community in Guinea was observed to increase their usage of tools during periods of fruit scarcity during a 13-month obervation period (Yamakoshi, 1998). Additionally, Tai chimpanzees tended to use tools to exploit nuts when the chimpanzees also tended to expend more energy than was gained. This effect was estimated by measuring the caloric and nutritional content of food from scraps found on the ground, and the daily movement of each individual (N'guessan, 2009). However, these observations of increased energy expenditures occurred during a time of overall resource abundance as defined by the relatively greater quantity of fruits available.

More puzzlingly, a meta-analysis of field studies in chimpanzees found that tool usage overall has no correlation with scarcity of preferred foods (Sanz and Morgan, 2013). These contradictory results suggest that additional processes may shape the evolution of tool use.

The opportunity hypothesis, in contrast, suggests that repeated exposure to specific environmental conditions that favor tool use prompts the evolution of tool usage behaviors. Appropriate environmental conditions that could elicit tool use include encounters with tool materials or exposure to prey. It is thought that Gombe chimpanzees use tools to gather termites opportunistically because this behavior occurs predominantly during rainy seasons, when both termites are more accessible and fruits are more abundant (Sanz and Morgan, 2013). In central Africa where termites are extremely common, field studies observed that chimpanzees developed tools to harvest termites year-round. However, in Seringbara, Guinea, termites are more rare, and no evidence of tool usage was found amongst *Pan troglodytes* here. Additionally, a long-term observation of a Goualougo chimpanzee population found no increase in tool use to compensate for lack of fruit resources. Instead, tools were utilized to access fallback food sources in accordance with the abundance of these food sources. In support of these results, measurements of resource location in relation to chimpanzee ranging patterns found that the density and distribution of nut trees contribute to the likelihood of tool use invention and transmission (Koops et al., 2013). Overall, while it is possible that both necessity and opportunity play a role in chimpanzee tool use, the wealth of available evidence strongly supports that the evolution of tool use in *Pan troglodytes* was predominantly influenced by opportunity.

Other Traits Affected Tool Use Evolution

While ecological opportunity is a necessary condition for tool use in *Pan troglodytes*, it is not sufficient. Almost all feeding tools used by *Pan troglodytes* are used in extractive foraging, and require some level of manipulative dexterity (van Schaik et al., 1999). Thus, in order for chimpanzees to evolve tool usage, they must have possessed sufficient dexterity of motor control in order to successfully handle tools. This is supported by findings from phylogenetic studies that primate species with greater motor control are more likely than less dexterous species to discover tool use. Additionally, motor skill in tool use was found to be heritable through quantitative genetic analyses of captive chimpanzees completing a precision tool-use task (Hopkins et. al., 2014). Thus, tool use is closely tied to fine motor dexterity in *Pan troglodytes,* a trait with an experimentally verified genetic basis. Because primates with greater motor control are more likely to use tools, the genes that contribute to dexterity are likely to be closely associated with the evolutionary development of tool use. It is possible that ecological opportunity provided the environmental stimulus for chimpanzees to draw from

While ecological opportunity, dexterity, and general intelligence provide the necessary substrate for an individual chimpanzee to utilize tools, certain social conditions must be in place in order for tool use to be transmitted between individuals. Because a new skill is only maintained in a population if it is able to spread beyond its inventor, transmission of tool use through social learning is critical to maintenance of the trait throughout *Pan troglodytes* communities (van Shaik et al., 1999). In order for social learning of tool use to occur, the primate species involved must form gregarious communities and feed in close proximity to each other. These qualifications present insight into why tool use became widespread in relatively few primate lineages; many species have solitary social structures, or do not feed in groups (van Schaik and van Noordwijk, 1986). Because social learning has been experimentally demonstrated to be a more efficient route of behavioral acquisition than learning by trial and error, primates capable of social learning are far more likely to develop

and transmit tool use (van Shaik et al., 1999). Thus, because *Pan troglodytes* societies had previously evolved gregariousness and social tolerance, this enabled chimpanzees to learn tool use from each other by imitation. This conclusion is supported by attempts to experimentally induce feeding tool manufacture in monkeys, which was most successful in more socially tolerant species (Tomasello and Call, 1997). This indicates that the origins of tool use cannot be entirely explained through ecological conditions, as the social environment of *Pan troglodytes* is also integral to the transmission and maintenance of tool usage. Thus, while certain ecological and genetic factors are necessary to make tool use possible in primates, the trait is unlikely to become widespread throughout a species without the social characteristics that allow for cultural transmission.

Effects of Chimpanzee Tool Use Evolution on Ecology

While few studies have been conducted that have explicitly documented the influence of chimpanzee tool use on its environment, many educated hypotheses can be drawn from the existing literature. Chimpanzee tools are thought to facilitate access to food that would be otherwise difficult to process (Boesch, 1989). For example, some chimpanzee communities have been observed to use stones to crack open *Detarium* nuts that fall on the ground. Chimpanzees that do not use stones to crack these nuts will leave the nuts on the ground for up to two months before eating the nuts whose shells have softened over time. These chimpanzees tend to be more selective with their nut consumption than chimpanzees who use stone tools, as tools permit them to consume the nuts as soon as they fall on the ground. Thus, it might be reasonable to assume that chimpanzee tool use limits the number of *Detarium* nuts that successfully grow to adult trees. Additionally, the use of sticks to gain access to bee or ant nests allows chimpanzees to sidestep the harmful stinging and biting defense mechanisms of these insects. This allows *Pan troglodytes* to increase their predation on these insects. Thus, it may be an interesting route of future study to determine if insect species have altered their defense mechanisms in a co-evolutionary response to chimpanzee tool use. Overall, while few studies have been conducted to quantify the affect of chimpanzee tool use on its environment, it is apparent that tool use allows chimpanzees to more easily access ants, termites, tree nuts, and other prey.

Conclusion

Identifying the evolution and ecology of tool use in *Pan troglodytes* sheds light on the origins of one of the behaviors most fundamental to understanding our own evolutionary history. Environmental factors such as the abundance of food sources requiring manipulative extraction provided the ecological opportunity necessary for the evolution of tool use. However, also critical for the origins of tool use are traits such as dexterity and intelligence, which allow *Pan troglodytes* to perform the precise manipulations necessary for tool use. Additionally, in order for tool usage to become prevalent throughout chimpanzee communities, a certain level of gregariousness and social tolerance is necessary to facilitate social learning of tool manipulations. These traits have also been previously shown to be heritable, highlighting the complex ways that ecology, genetics and culture intersect to affect evolution. However, the evolution of tool use in turn has affected the environment of the species, as chimpanzees are able to use tools to bypass the evolutionary defenses of trees and insects against predation. However, a promising route of future study would be to investigate if the fitness of ants, termites, or nut trees that share habitats with *Pan troglodytes* is less than the fitness of such food sources that do not co-habit geographic regions with tool-using primates. Such a study might be executed by introducing tool-using chimpanzee populations

into a new controlled habitat with army ant populations, and observing if the number of army ants in this habitat declines compared to populations in habitats with non-tool-using primates. This would experimentally verify that chimpanzee tool manipulation has a quantifiable impact on its environment. Overall, tool usage by *Pan troglodytes* is a fascinating trait that encompasses many areas of study. Its rich evolutionary history and complex ecological interactions will likely be a source of continuing scientific inquiry for years to come.

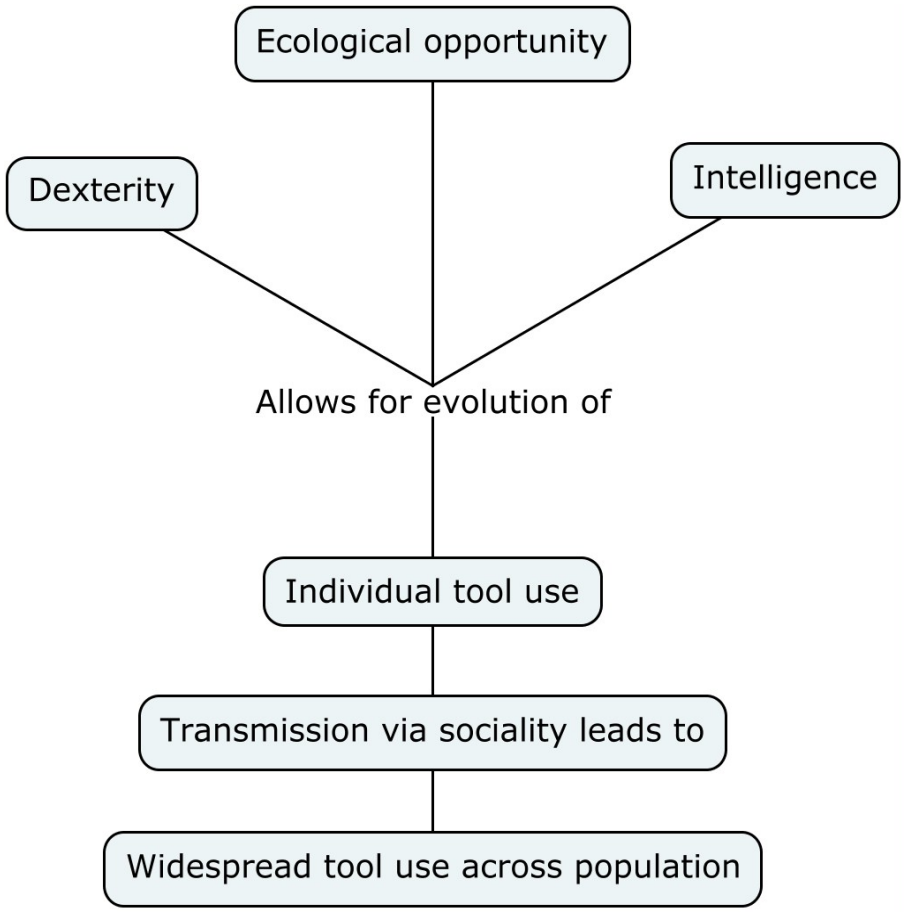

Fig. A. Ecological opportunity, intelligence, and dexterity provide the environmental and physiological substrate necessary for tool use. Sociality and social learning allow for tool use to become spread throughout a chimpanzee population via cultural transmission.

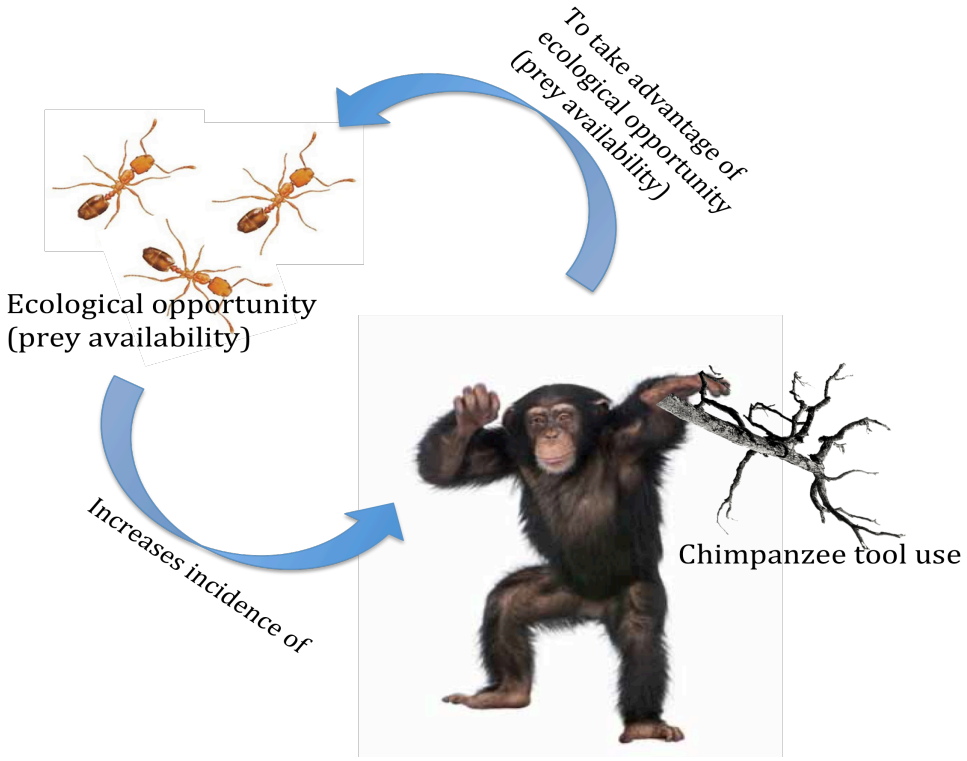

Fig. B. Ecological opportunity, primarily defined by the availability of prey, increases chimpanzee tool use.

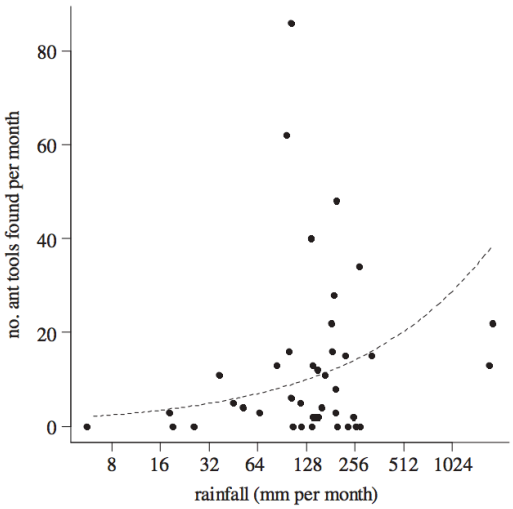

Fig. C: Chimpanzee tool use for ant foraging correlates positively with rainfall, which increases ant accessibility.

References

BIRO, D., HASLAM, M. & RUTZ, C. 2013. Tool use as adaptation. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 368.

BOESCH, C. 1991. TEACHING AMONG WILD CHIMPANZEES. *Animal Behaviour,* 41**,** 530-532.

BOESCH, C. & BOESCH, H. 1989. HUNTING BEHAVIOR OF WILD CHIMPANZEES IN THE TAI-NATIONAL-PARK. *American Journal of Physical Anthropology,* 78**,** 547-573.

BOESCH, C. & BOESCH, H. 1990. TOOL USE AND TOOL MAKING IN WILD CHIMPANZEES. *Folia Primatologica,* 54**,** 86-99.

BRENT, L. J. N., HEILBRONNER, S. R., HORVATH, J. E., GONZALEZ-MARTINEZ, J., RUIZ-LAMBIDES, A., ROBINSON, A. G., SKENE, J. H. P. & PLATT, M. L. 2013. Genetic origins of social networks in rhesus macaques. *Scientific Reports,* 3.

HARRISON, M. E. & MARSHALL, A. J. 2011. Strategies for the Use of Fallback Foods in Apes. *International Journal of Primatology,* 32**,** 531-565.

HOPKINS, W. D., REAMER, L., MARENO, M. C. & SCHAPIRO, S. J. 2015. Genetic basis in motor skill and hand preference for tool use in chimpanzees (Pan troglodytes). *Proceedings of the Royal Society B-Biological Sciences,* 282**,** 7.

KOOPS, K., MCGREW, W. C. & MATSUZAWA, T. 2013. Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, Pan troglodytes verus? *Animal Behaviour,* 85**,** 175-185.

KOOPS, K., VISALBERGHI, E. & VAN SCHAIK, C. P. 2014. The ecology of primate material culture. *Biology Letters,* 10.

N'GUESSAN, A. K., ORTMANN, S. & BOESCH, C. 2009. Daily Energy Balance and Protein Gain Among Pan troglodytes verus in the Ta < National Park, CA ' te d'Ivoire. *International Journal of Primatology,* 30**,** 481-496.

NISHIDA, T. & HIRAIWA, M. 1982. NATURAL-HISTORY OF A TOOL-USING BEHAVIOR BY WILD CHIMPANZEES IN FEEDING UPON WOOD-BORING ANTS. *Journal of Human Evolution,* 11**,** 73-99.

SANZ, C. M. & MORGAN, D. B. 2013. Ecological and social correlates of chimpanzee tool use. *Philosophical Transactions of the Royal Society B-Biological Sciences,* 368.

VAN SCHAIK, C. P., DEANER, R. O. & MERRILL, M. Y. 1999. The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution,* 36**,** 719-741.

VAN SCHAIK, C. P. & PRADHAN, G. R. 2003. A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. *Journal of Human Evolution,* 44**,** 645-664.

YAMAKOSHI, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. *American Journal of Physical Anthropology,* 106**,** 283-295.